

Long-term development of above- and below-ground carbon stocks following land-use change in subalpine ecosystems of the Swiss National Park

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Abstract: Vegetation changes following agricultural land abandonment at high elevation—which is frequent in Europe—could have a major impact on carbon (C) sequestration. However, most information on the effects of vegetation changes on ecosystem C stocks originates from low-elevation studies on reforestation or early successional forests, and little is known about how these stocks change during long-term secondary forest succession and at high elevation. We assessed aboveground, belowground, and ecosystem organic matter and C stocks in high-elevation ecosystems that represent the long-term development (centuries) following land abandonment: short- and tall-grass pastures, Swiss mountain pine (*Pinus mugo* Turra), mixed-conifer, and Swiss stone pine (*Pinus cembra* L.)–European larch (*Larix decidua* P. Mill.) forests. Aboveground C stocks were lowest in the short-grass pastures (0.1 Mg C·ha⁻¹) and reached a maximum in the mixed-conifer and stone pine–larch forests (166 Mg C·ha⁻¹). Belowground C stocks did not differ among the ecosystems studied. We only detected ecosystem C sequestration during reforestation; whereas no significant differences in ecosystem C stocks were found during long-term secondary forest development. Our calculations showed that only an additional 1733–3032 Mg C·year⁻¹ would be sequestered owing to natural reforestation in high-elevation Switzerland, which likely can be considered negligible compared with total annual C sequestration calculated for Swiss forests in other studies.

Résumé : Les changements qui surviennent dans la végétation à la suite de l'abandon des terres agricoles situées à haute altitude, ce qui est fréquent en Europe, pourraient avoir un impact majeur sur la séquestration du carbone (C). Cependant, la majeure partie des informations qui existent concernant les effets sur les stocks de C des écosystèmes provient d'études réalisées à basse altitude à la suite d'un reboisement ou dans des forêts aux premiers stades de succession. On connaît peu de chose au sujet de l'évolution à long terme des stocks de C en cours de succession dans la forêt de seconde venue et des forêts situées à haute altitude. Nous avons évalué la matière organique et les stocks de C au-dessus du sol, dans le sol et pour l'ensemble de l'écosystème dans des écosystèmes situés à haute altitude qui correspondent à des stades de développement à long terme (siècles) de la végétation à la suite de l'abandon des terres : pâturages d'herbes basses et pâturages d'herbes hautes, pin de montagne (*Pinus mugo* Turra), forêts mélangées de conifères et forêts de mélèze (*Larix decidua* P. Mill.) et de pin cembro-mélèze (*Pinus cembra* L.). Les stocks aériens étaient le plus faible chez les petites graminées (0,1 Mg C·ha⁻¹) et culminaient dans les forêts mélangées de conifères et les forêts de pin cembro (166 Mg C·ha⁻¹). Les stocks de C dans le sol n'étaient pas différents peu importe l'écosystème étudié. La séquestration de C par l'écosystème a été détectée seulement lors du reboisement, alors qu'aucune différence significative dans les stocks de C de l'écosystème n'a été observée au cours du développement à long terme de la forêt secondaire. Nos calculs montrent que seulement 1733–3032 Mg C·an⁻¹ additionnels seraient séquestrés à cause du reboisement naturel à haute altitude en Suisse, ce qui peut probablement être considéré comme négligeable comparativement à la séquestration annuelle totale de C calculée pour les forêts suisses dans d'autres études.

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Introduction

Terrestrial ecosystems play an important role in the global carbon (C) cycle, serving as both C sinks and sources (Schimel 1995). Approximately half of the organic C stored in these ecosystems is sequestered by forests (Dixon et al. 1994). During the past decades, the total forested area and the amount of woody biomass (organic matter (OM)) has increased in both North America and Europe (e.g., Liski et al. 2003) as a consequence of farmland and pasture abandonment (e.g., Thuille and Schulze 2006), fire suppression (e.g., Page-Dumroese et al. 2003), and improved tree growth due to global warming and nutrient deposition (e.g., Kauppi et al. 1992; Melillo et al. 1996). In Europe, changes in economic policies have reduced traditional agricultural (live-stock grazing, hay production) and intensive forest management practices (thinning, fertilization), which resulted in increased forest cover, especially at elevations >1650 m a.s.l. (e.g., Höchtl et al. 2005; Tasser et al. 2007). Even though high-elevation ecosystems make up >40% of the land base in Europe (Nordic Center for Spatial Development Nordregio 2004), these ecosystems have only recently gained attention in the discussion of global C cycling (e.g., Rodeghiero and Cescatti 2005; Thuille and Schulze 2006; Gamper et al. 2007).

Most studies conducted on land-use changes on both low- and high-elevation sites in Europe have indicated that aboveground OM and C stocks increase during reforestation of abandoned farmland or pastures (e.g., Thuille et al. 2000; Thuille and Schulze 2006). In contrast, belowground OM and C stock changes during reforestation of abandoned farmland and pastures are more controversial (see review by Jandl et al. 2007), as increases, decreases, and insignificant changes have been reported (e.g., Smith et al. 1997; Thuille and Schulze 2006). Even less is known about how OM and C stocks change during long-term secondary forest succession, as all the studies we are aware of have focused on chronosequences of early successional forest communities (e.g., Thuille and Schulze 2006; Cerli et al. 2006), and therefore did not account for possible changes in C stocks that occur in the later stages of forest succession. Such subsequent long-term changes in both above- and below-ground C stocks could, however, be an important factor in selecting management scenarios for C sequestration in high-elevation forests. Therefore, the objective of this study was to determine OM and C stocks in high-elevation pastures and forests that represent five different ecosystem stages of a long-term succession pattern following land abandonment in the Central European Alps.

Methods

Study area

The Swiss National Park (SNP) is located in the south-eastern part of Switzerland and covers an area of 170 km², 50 km² of which are forested and 3 km² of which are occupied by subalpine pastures. Elevation ranges from 1350 to 3170 m a.s.l., and mean annual precipitation and temperature are 925 ± 162 mm and 0.2 ± 0.7 °C (mean ± SD), respectively, measured at the Park's weather station in Buffalora (1980 m a.s.l.) between 1904 and 1994. Founded in 1914, the SNP was not managed for most of the 20th cen-

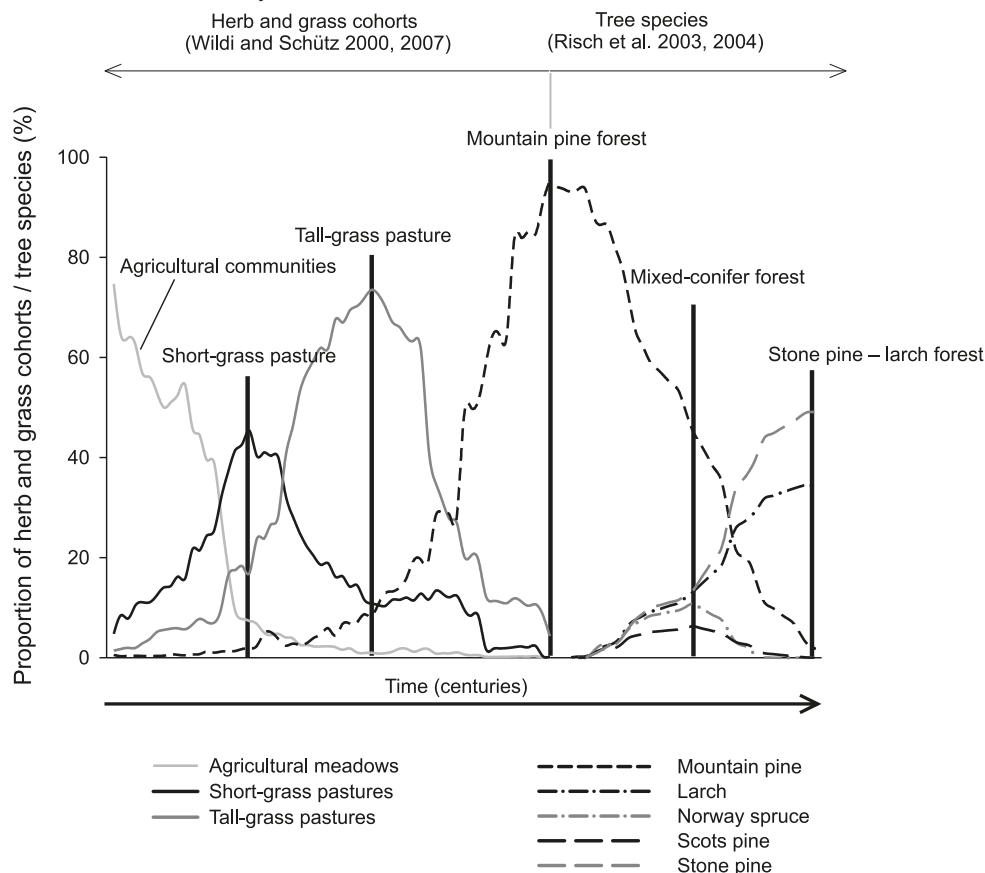
tury. However, records of timber harvesting date back to the 14th century, when forests were cut to support the development of a local iron-ore industry. Additional harvesting occurred during the 17th, 18th, and 19th centuries, to supply charcoal for lime-kilns and timber for use in a nearby salt mine. Clear-cutting forest stands for agricultural use (cattle and sheep grazing, hay production) began as early as the 15th century, and many pastures were used until the SNP was established in 1914 (Parolini 1995).

The long-term development of the ecosystems within SNP has been studied in detail using data from time series from permanent plots that date as far back as 1917. By overlaying these time series in a space-for-time approach (Pickett 1989), we determined the order of ecosystem stages in time (Wildi and Schütz 2000, 2007; Risch et al. 2003, 2004). Based on the overlay, we then delineated five temporally distinct ecosystem states, hereinafter referred to as ecosystem types (Fig. 1):

1. short-grass pastures dominated by red fescue (*Festuca rubra* L.), perennial quaking grass (*Briza media* L.), and milfoil (*Achillea millefolium* L.);
2. tall-grass pastures dominated by evergreen sedge (*Carex sempervirens* Vill.), mat-grass (*Nardus stricta* L.), and Bellard's Kobresia (*Elyna myosuroides* (Vill.) Fritsch);
3. Swiss mountain pine (*Pinus mugo* Turra; hereinafter mountain pine) forests;
4. mixed-conifer stands of mountain pine, Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* P. Mill.; hereinafter larch), and Swiss stone pine (*Pinus cembra* L.; hereinafter stone pine);
5. stone pine – larch stands

Transitions between these stages have been observed at least once or even several times in the permanent plots; thus, the model confirms the chronological order of the stages. Short-grass pastures developed on former cattle pastures, which became preferred grazing sites for red deer (*Cervus elaphus* L.) after abandonment (Schütz et al. 2006). When grazing pressure by red deer decreased, tall-grass pastures developed (Wildi and Schütz 2000; Schütz et al. 2006). The mountain pine forests are early-successional forests in which self-thinning (stem exclusion) is the dominant process (Risch et al. 2003, 2004). In the mixed-conifer stands, vertical and horizontal diversification are the underlying ecological processes, during which the monodominant pioneer tree layer composed of mountain pine is replaced by a mixed-tree layer that contains larch, Norway spruce, Scots pine, and, to a lesser extent, stone pine (Risch et al. 2003). Further diversification leads to stands dominated by stone pine – larch. These forests are considered the late-successional stage, in which the shade-intolerant pioneer mountain pine is no longer present (loss of pioneer cohort; Franklin et al. 2002; Fig. 1). It is difficult to predict the speed of the vegetation changes outlined above, as it depends on site conditions (e.g., elevation, nutrient availability, disturbance) and the method used to calculate the similarity of the time patterns retrieved from the permanent plots (Wildi and Schütz 2007). However, based on calculations for the early stages of the series (short-grass pasture to mountain pine

Fig. 1. Successional development from abandoned agricultural communities to stone pine–larch forests in the Swiss National Park (SNP). The development is based on an overlay of time series data (space-for-time approach: development of agricultural communities to mountain pine forest (Wildi and Schütz 2000, 2007) and from mountain pine forest to stone pine–larch stands (Risch et al. 2003, 2004)). Bars indicate the five ecosystem states chosen for study.



forest; Wildi and Schütz 2007), it can be assumed that likely over half a millenium would pass during succession from short-grass pasture to stone pine–larch stands.

Sampling design

Three short-, two tall-grass pastures, and 18 forest stands from the three forest development stages (six mountain pine, five mixed-conifer, seven stone pine–larch) were selected for study (23 sites in total). Only two tall-grass pastures were selected, since all other accessible subalpine grasslands have short-grass vegetation. All pastures and mountain pine forests were located on south-facing slopes, while the mixed-conifer and stone pine–larch stands were found on slopes facing all cardinal directions. The soil parent material for all pastures, mountain pine forests, mixed-conifer stands, and three of seven stone pine–larch stands is calcareous moraines and rubble. Four other stone pine–larch stands were found on acidic verrucano-dominated moraines and rubble. All pasture and forest sites were located between 1800 and 2050 m a.s.l., and are part of larger studies on ecosystem productivity or long-term forest development (Risch et al. 2003, 2004; Thiel-Egenter et al. 2007).

Field sampling

Pastures

We estimated aboveground pasture biomass in late July

2001 by clipping the vegetation to a height of 2 cm on 50 systematically selected 48 cm × 28 cm areas per pasture (Thiel-Egenter et al. 2007). Vegetation relevés (record of plant species composition) were conducted before clipping, and the cover (%) of each species recorded; species names followed Lauber and Wagner (2001). Soil surface organic layer (SOL) and mineral soil were sampled on 3–15 randomly selected plots (20 m × 20 m grid; see Schütz et al. 2006) per pasture (sample number depended on pasture size; 2–10 ha). Owing to the high rock content in the sub-soil, mineral soil samples were taken only to a depth of 20 cm. Soil bulk density was determined using the polyurethane foam technique (Page-Dumroese et al. 1999).

Forest stands

Systematic grids of 70 m × 70 m or 40 m × 40 m (1.4–4.4 ha) were established in the center of each forest stand, depending on total stand area (Risch et al. 2003, 2004). Tree (>130 cm tall, alive and dead) and sapling (21–130 cm tall) species composition and density were measured on 16 grid-points per stand using the point-centered quarter method in 2001 (see Risch et al. 2003, 2004). Species, diameter at breast height (DBH = 130 cm), and total height (measured using a clinometer) were recorded for the closest tree and sapling in each quarter at each of the 16 points (four trees and four saplings at each point in total). Stem increment cores were taken from two of the four trees at each

point (at DBH), and stand age was estimated as the mean age of the 15 oldest trees found within each stand. Five additional stem increment cores and five foliage samples of each tree species were collected in the different forest types for C analyses. The degree of stand canopy closure was measured with a densiometer by taking four measurements in all cardinal directions around the center of each sampling point (see Risch et al. 2003, 2004). A vegetation relevée was conducted on a 10 m × 10 m plot established at the center of each stand, and the cover (%) of each species recorded. In addition, seven saplings (20, 40, 60, 80, 100, 120, and 130 cm tall) of each species were collected throughout the study area to develop allometric biomass equations for saplings.

All understory vegetation (<20 cm tall) and the SOL (including pine cones) were removed from three 700 cm² circular plots located on three sides of each 10 m × 10 m plot and kept separate for further analyses. Mineral soil samples were then taken to a depth of 20 cm with hand trowels, and total bulk density was estimated using the polyurethane foam technique (Page-Dumroese et al. 1999). Fine-fraction soil bulk density was calculated using volumetric and gravimetric rock-fragment content. We assumed rock-fragment density was 2.65 Mg·m⁻³. Mineral soil C stocks were corrected for coarse-fragment content and extrapolated to a hectare basis using the fine-fraction bulk density.

The amount of nonstanding dead woody residue was measured along three 16.5 m transects in each stand using a planar intersect method (for more detail see Risch et al. 2003, 2004). Ten woody residue samples (five solid and five rotten) were taken in each stand type for C analyses. Woody residue <0.6 cm diameter was not sampled, but was included in the SOL samples.

Laboratory analyses

All aboveground pasture biomass and forest stem, foliage, understory vegetation, woody residue, and SOL samples were oven-dried at 65 °C, and fine-ground to pass through a 0.5 mm mesh screen. Mineral soil samples were oven-dried at 105 °C to constant mass and passed through a 2 mm mesh sieve. Roots (hereinafter referred to as fine roots) were separated from the >2 mm material, weighed, and ground to pass through a 0.5 mm mesh screen. Mineral soil samples from the calcareous moraine and rubble parent material were treated with a 50% hydrochloric acid solution to remove carbonates, and then dried for 1–2 h before analysis. All organic and soil samples were analyzed for C on a LECO induction furnace at 1000 °C (LECO Corp., St. Joseph, Michigan). The OM content of the mineral soil and SOL were determined by loss-on-ignition at 425 °C. Mineral soil pH was measured on a 2:1 water soil paste, and soil texture was determined using the hydrometer method. Available water was calculated after determining permanent wilting point and field capacity using the pressure plate method.

Calculation of OM and C stocks

Since the study was performed in a national park, we were unable to destructively sample whole trees (>130 cm tall). Therefore, we used allometric equations developed from the Swiss National Forest Inventory (SNFI) to calculate stem, branch, foliage, and coarse root biomass for individual stands (Kramer 1982; Perruchoud et al. 1999; Kaufmann 2001, 2002). Equation 1 was used to calculate biomass for standing trees, both living and dead, with DBH >7.5 cm (Bio_{large}).

$$[1] \quad \text{Bio}_{\text{large}} = \sum_{i=1}^n \sum_{j=1}^m (a_{0,i} + a_{1,i} \text{DBH}_{i,j}^2 H_{i,j} + a_{2,i} \text{DBH}_{i,j}^3 H_{i,j}) \times \text{stems}_{i,j} \text{sg}_i$$

where i is the tree species, j is the diameter class, $\text{DBH}_{i,j}$ is the mean diameter of species i in diameter class j (cm), $H_{i,j}$ is the mean height of species i in diameter class j (cm) and $\text{stems}_{i,j}$ is the number of stems of species i in diameter class j . The same variables are also used in eqs. 2–5. The variables $a_{0,i}$, $a_{1,i}$, and $a_{2,i}$ are regression parameters (Appendix A, Table A1) and sg_i is the basic density (dry mass per fresh volume) of species i (g·cm⁻³) (Appendix A, Table A1).

For trees with DBH between 0.5 and 7.5 cm (Bio_{small}), we used eq. 2 for a paraboloid

$$[2] \quad \text{Bio}_{\text{small}} = \sum_{i=1}^n \sum_{j=1}^m \left(\frac{1}{2} \pi \text{DBH}_{i,j}^2 H_{i,j} \text{sg}_i \right) \times \text{stems}_{i,j}$$

Total branch and twig biomass (Bio_{branches}) was calculated by adding branch and twig biomass calculated using eq. 3 and total foliage biomass (Bio_{foliage}) was estimated with eq. 4. Regression parameters a_i , b_i , $b_{0,i}$, $b_{1,i}$, $b_{2,i}$, $b_{3,i}$, c_i , $h_{1,i}$, and $h_{2,i}$ can be found in Appendix A, Table A1.

$$[3] \quad \text{Bio}_{\text{branches}} = \sum_{i=1}^n \sum_{j=1}^m (b_{0,i} + b_{1,i} \text{DBH}_{i,j} + b_{2,i} h_{1,i} + b_{3,i} h_{2,i}) \times \text{stems}_{i,j} \text{sg}_i$$

$$[4] \quad \text{Bio}_{\text{foliage}} = \sum_{i=1}^n \sum_{j=1}^m (a_i + b_i \text{DBH}_{i,j}^2 + c_i \text{DBH}_{i,j}^4) \times \text{stems}_{i,j}$$

Table 1. Pasture vegetation composition (%), aboveground biomass, and aboveground C stocks (Mg·ha⁻¹) in short- and tall-grass pastures studied in the Swiss National Park (SNP).

Ecosystem type	Cover (%)					Aboveground biomass (Mg·ha ⁻¹)	C stock (Mg·ha ⁻¹)
	Herbs*	Grasses*	Sedges	Mosses*	Ericaceous plants*		
Short-grass	50 (7)	38 (9)	11 (7)b	—	—	0.3 (0.1)b	0.1 (0.1)b
Tall-grass	54 (4)	21 (6)	31 (7)a	—	—	3.0 (1.0)a	1.3 (0.5)a

Note: Coverage totals can add up to >100%, as several layers were added. Values in parentheses are SEs. Values followed by the same lowercase letter are not significantly different ($p = 0.05$).

*Not significantly different.

Table 2. Forest understory (% cover) and overstory (% of total basal area (BA)) composition, total BA (m²·ha⁻¹), stand density (stems·ha⁻¹), stand height (m), canopy closure (%), and stand age (years) for the forest types studied in the SNP.

(A) Understory composition (% cover).

Ecosystem type	Herbs*	Grasses	Sedges*	Mosses	Ericaceous shrubs		
					Total	<i>E. carnea</i>	Others* [†]
Mountain pine	6 (1)	5 (1)b	5 (2)	9 (4)ab	67 (5)a	52 (8)a	15 (2)
Mixed-conifer	10 (3)	30 (17)ab	<1 (<1)	2 (1)b	46 (14)a	38 (16)a	9 (4)
Stone pine–larch (alkaline)	11 (3)	39 (8)a	11 (10)	1(<1)b	8 (6)b	3 (3)b	5 (3)
Stone pine–larch (acidic)	4 (1)	4 (2)b	0 (0)	19 (7)a	23 (8) b	0 (—)b	23 (8)

(B) Overstory composition (% total BA).

Ecosystem type	<i>Pinus montana</i>	<i>Pinus cembra</i>	<i>Larix decidua</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>
Mountain pine	96 (3)	2 (2)	1 (1)	—	1 (1)
Mixed-conifer	17 (1)	1 (1)	32 (7)	34 (9)	16 (6)
Stone pine–larch (alkaline)	7 (4)	49 (13)	44 (10)	—	—
Stone pine–larch (acidic)	4 (2)	60 (10)	30 (12)	6 (6)	1 (1)

(C) Overstory structural features.

Ecosystem type	BA (m ² ·ha ⁻¹)	Height (m)	Density (stems·ha ⁻¹)	Canopy closure (%)	Age (years)
Mountain pine	25 (4)b	13 (<1)b	1350 (227)a	43 (4)c	156 (10)
Mixed-conifer	42 (2)a	24 (2)a	791 (54)b	54 (3)bc	187 (5)
Stone pine–larch (alkaline)	44 (3)a	23 (1)a	473 (73)b	70 (7)a	223 (24)
Stone pine–larch (acidic)	50 (8)a	25 (1)a	473 (90)b	65 (3)ab	223 (18)

Note: Coverage totals can add up to >100%, as several layers were added. Values in parentheses are SEs. Values followed by the same lowercase letter are not significantly different ($p = 0.05$).

*Not significantly different.

[†]*Vaccinium myrtillus*, *Vaccinium vitis-idea*, *Rhododendron ferrugineum*.

Equation 5 was used for calculating coarse root biomass (Bio_{roots}) using $a_3 = -0.371467$, $a_4 = 0.003077$, and $a_5 = -0.000005217$.

$$[5] \quad \text{Bio}_{\text{roots}} = \sum_{j=1}^m (a_3 + a_4 \text{DBH}_j^3 + a_5 \text{DBH}_j^4 + 48.796249) \times \text{stems}_j$$

We then calculated OM and C stocks for each pasture and forest stand by multiplying the biomass of each component with its respective OM or C concentration found in Appendix B, Tables B1 and B2 (tree species-specific calculations were made based on stand composition). Mineral soil C was calculated based on fine-fraction soil bulk density (see Page-Dumroese et al. 1999). We then summed up all components to obtain (i) aboveground (living and dead trees, branches, foliage, woody residue, saplings, understory vegetation), (ii) belowground (mineral soil, SOL, coarse and fine roots), and (iii) ecosystem (aboveground and belowground) OM and C stocks. Finally, we averaged the stocks for each pasture type (short- and tall-grass) and for each of the three forests

types, while distinguishing between alkaline and acidic stone pine–larch forests (hereinafter referred to as “mountain pine,” “mixed-conifer,” “alkaline stone pine–larch,” and “acidic stone pine–larch”).

Statistical analyses

We used *t*-tests to assess whether percent cover of herbs, grasses, sedges, ericaceous shrubs, and mosses differed between the two pasture types and one-way ANOVAs followed by Tukey's post-hoc test to assess the differences among the four forest stand types ($p = 0.05$). One-way ANOVAs followed by a Tukey's post-hoc test were also used to test differences in forest stand type properties (basal

Table 3. Forest stand biomass ($\text{Mg}\cdot\text{ha}^{-1}$) and C ($\text{Mg}\cdot\text{ha}^{-1}$) stocks within the forest types studied in the SNP.

Ecosystem type	Stems	Branches	Foliage	Standing dead trees*	Woody residue*	Understory vegetation	Total†
Biomass ($\text{Mg}\cdot\text{ha}^{-1}$)							
Mountain pine	106 (16)b	12 (2)b	4 (1)b	19 (5)	33 (13)	5 (1)a	179 (11)b
Mixed-conifer	234 (32)a	16 (3)ab	7 (<1)a	10 (3)	60 (22)	4 (1)ab	331 (48)a
Stone pine – larch (alkaline)	259 (56)a	23 (4)a	5 (<1)b	11 (3)	21 (7)	1 (<1)c	320 (59)a
Stone pine – larch (acidic)	258 (35)a	22 (2)a	6 (1)a	11 (3)	26 (6)	2 (1)bc	325 (41)a
C ($\text{Mg}\cdot\text{ha}^{-1}$)							
Mountain pine	54 (8)b	6 (1)b	2 (<1)c	9 (2)	17 (7)	2 (<1)a	90 (6)b
Mixed-conifer	116 (16)a	8 (2)ab	4 (<1)a	5 (2)	31 (11)	2 (<1)ab	166 (24)a
Stone pine – larch (alkaline)	131 (27)a	11 (2)a	3 (<1)bc	6 (2)	11 (3)	1 (<1)bc	163 (29)a
Stone pine – larch (acidic)	131 (17)a	11 (1)a	3 (1)ab	6 (2)	14 (3)	1 (<1)bc	166 (20)a

Note: Values in parentheses are SEs. Values followed by the same lowercase letter are not significantly different ($p = 0.05$).

*Not significantly different.

†Sapling biomass and C stocks are not shown, as values were only between 0.14 and 0.02 $\text{Mg OM}\cdot\text{ha}^{-1}$ and 0.07 and 0.01 $\text{Mg C}\cdot\text{ha}^{-1}$, respectively.

Table 4. Selected soil physical and chemical properties from the ecosystem types studied in the SNP.

Ecosystem type	Texture	Bulk density ($\text{Mg}\cdot\text{m}^{-3}$)	Rock content (%)*	OM (%)	C (%)	pH	Available water ($\text{g}\cdot 100\text{ g}^{-1}$ soil)*
Short-grass pasture	Loamy sand	1.03 (0.06)b	22 (6)	14.9 (2.7)a	8.3 (1.5)a	6.5 (0.3)a	9.4 (1.6)
Tall-grass pasture	Loamy sand	1.13 (0.13)ab	27 (12)	10.6 (0.9)ab	6.0 (1.0)ab	5.6 (1.5)a	8.3 (1.3)
Mountain pine	Sandy loam	1.25 (0.13)ab	32 (4)	13.5 (1.5)a	8.6 (1.3)a	6.2 (0.1)a	11.5 (1.5)
Mixed-conifer	Loamy sand	1.36 (0.10)ab	30 (3)	7.3 (0.8)b	3.6 (0.3)bc	5.5 (0.5)a	12.2 (1.7)
Stone pine – larch (alkaline)	Sandy loam	1.08 (0.11)b	21 (2)	8.1 (0.8)b	4.2 (0.3)bc	5.3 (0.4)a	14.5 (1.2)
Stone pine – larch (acidic)	Sand	1.57 (0.13)a	37 (7)	3.2 (0.7)c	2.0 (0.4)c	3.1 (0.2)b	10.6 (1.3)

Note: Values in parentheses are SEs. Values followed by the same lowercase letter are not significantly different ($p = 0.05$).

*Not significantly different.

area (BA), canopy closure). We also used t -tests to assess differences in aboveground C and OM stocks between the two pasture types and one-way ANOVAs followed by Tukey's post-hoc test for testing differences among living and dead stem, foliage, branch, understory, and aboveground OM and C stocks in the forest types. Differences in mineral soil C content, physical properties (texture, bulk density, rock content, OM content, pH, available water content), as well as mineral soil, SOL, fine root, coarse root, and woody residue OM and C stocks, and total belowground and ecosystem stocks among the different ecosystem types were again tested with one-way ANOVA followed by Tukey's post-hoc test. The homogeneity criteria were met for all data. With the exception of the variable "vegetation cover," we used untransformed data for the analyses, since the normality criteria were met. Vegetation cover was arcsin square root transformed.

Results

Aboveground stocks

Grasses and herbs dominated the short-grass pastures, while sedges were more prevalent in the tall-grass pastures (Table 1). In contrast, ericaceous shrubs were the dominant understory vegetation in the forest ecosystems, except in the alkaline stone pine – larch stands, where grasses and herbs prevailed (Table 2). Approximately 80% of the total ericaceous shrub cover in both the mountain pine forests and mixed-conifer stands was winter heath (*Erica carnea* L., while the Ericaceae community in the acidic stone pine – larch forests comprised myrtle blueberry (*Vaccinium myrtillus*

L.), lingonberry (*V. vitis-idaea* L.), and rusty leaved Alpenrose (*Rhododendron ferrugineum* L.).

Aboveground OM (biomass) and C stocks in the tall-grass pastures were much larger than in the short-grass pastures (Table 1) and were a function of mean vegetation height: 16 cm in the tall-grass pastures versus 2 cm in the short-grass pastures (unpublished data). Even though the mountain pine stands had the highest numbers of trees $\cdot\text{ha}^{-1}$, aboveground OM and C stocks were the lowest of all forest types, which was a result of small tree diameters, low BA, and low mean stand height (Tables 2 and 3). Aboveground OM and C stocks did not significantly differ between the mixed-conifer and the stone pine – larch stands. Parent material did not affect stand growth in the stone pine – larch stands, as both acidic and alkaline stands had similar amounts of aboveground biomass. Standing dead trees and woody residue stocks did not significantly differ among the forest types (Tables 2 and 3).

Belowground stocks

Fine-fraction soil bulk density varied considerably among the ecosystem types, but no pattern was evident except that soils with the highest bulk densities (acidic stone pine – larch stands) were very acidic (Table 4). No difference in soil acidity was found among the two pasture types and the forest types with calcareous parent material. Rock contents and water availability were similar among the pasture and forest soils. Mineral soil C concentrations and stocks were highest in the mountain pine forests, but only significantly differed from the mixed-conifer and stone pine – larch stands (Tables 4

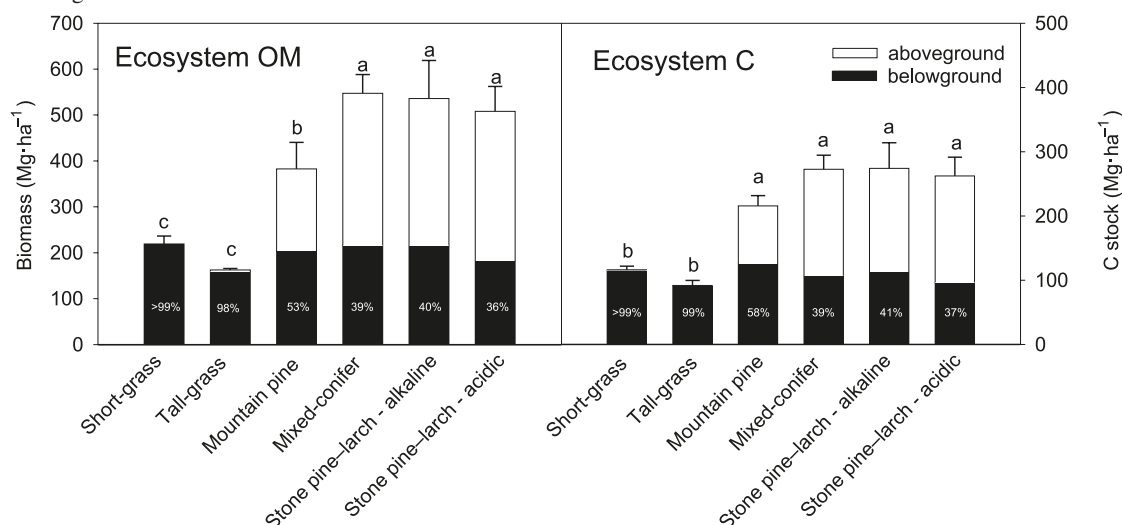
Table 5. Belowground biomass ($\text{Mg}\cdot\text{ha}^{-1}$) and C ($\text{Mg}\cdot\text{ha}^{-1}$) stocks within the ecosystem types studied in the SNP.

Ecosystem type	Mineral soil	Surface organic layer*	Fine roots*	Coarse roots	Total*
Organic matter ($\text{Mg}\cdot\text{ha}^{-1}$)					
Short-grass	156 (12)a	53 (20)	11 (4)	—	220 (17)
Tall-grass	109 (15)a	46 (15)	5 (2)	—	160 (2)
Mountain pine	138 (19)a	43 (9)	4 (1)	19 (3)b	204 (20)
Mixed	112 (18)a	29 (11)	7 (2)	68 (8)a	216 (22)
Stone pine – larch (alkaline)	101 (2)a	34 (16)	7 (2)	73 (9)a	215 (24)
Stone pine – larch (acidic)	46 (3)b	41 (18)	6 (5)	89 (15)a	182 (23)
C ($\text{Mg}\cdot\text{ha}^{-1}$)					
Short-grass	84 (5)ab	27 (9)	4 (2)	—	115 (7)
Tall-grass	66 (2)ab	23 (8)	2 (1)	—	91 (8)
Mountain pine	91 (13)a	23 (5)	2 (<1)	9 (2)b	125 (16)
Mixed	54 (6)bc	16 (6)	3 (1)	34 (4)a	107 (7)
Stone pine – larch (alkaline)	54 (5)bc	19 (9)	3 (1)	36 (4)a	112 (11)
Stone pine – larch (acidic)	29 (3)c	20 (7)	3 (2)	45 (7)a	97 (2)

Note: Values in parentheses are SEs. Values followed by the same lowercase letter are not significantly different ($p = 0.05$).

*Not significantly different.

Fig. 2. Total above- and below-ground biomass (OM) and C stocks for the ecosystem types studied in the SNP. Bars with the same lowercase letter are not significantly different ($p = 0.05$). Error bars represent total ecosystem stock SE. Percentage values (%) are belowground stocks as a percentage of total stocks.



and 5). Fine roots and SOL stocks were not significantly different among the six pasture and forest ecosystem types under study. Since coarse root biomasses were calculated from aboveground tree biomass values, coarse root OM and C stocks increased with aboveground biomass. To our surprise, high mineral soil C contents in the mountain pine forests compensated for coarse root biomass in the other forest types, so we found no significant differences in total belowground OM and C stocks among the ecosystem types under study. Approximately 73% of the belowground C was stored in the mineral soil of the pastures and the mountain pine forests compared with ~50% in the mixed-conifer and alkaline stone pine–larch stands, and 30% in the acidic stone pine–larch stands.

Ecosystem stocks

When above- and below-ground OM and C stocks were combined (Fig. 2), forests had significantly higher totals than pastures (OM, $p < 0.001$; C, $p = 0.009$). However,

increased aboveground and root biomass stocks in later successional forest stands (mixed-conifer and stone pine–larch stands) were offset by lower soil C levels, resulting in no differences in total C stock among forest stands. Thus, only reforestation of former pastures by mountain pine would sequester C, and no net C sequestration would occur during secondary forest development at these high-elevations. The fraction of ecosystem C stored in aboveground biomass (stem, branches, foliage, woody residue, saplings, understory vegetation) in the forest ecosystems was higher in the mixed-conifer and stone pine–larch stands compared with the mountain pine stands (Fig. 2). Root/stem C stock ratios increased from 20% in the mountain pine stands to 30%–37% in the other forest stand types.

Discussion

C stocks

Not surprisingly, our study showed large differences in

Table 6. Carbon (C) stocks of high-elevation forests in the SNP and in other high-elevation areas of Europe.

Vegetation	No. of stands	Elevation (m a.s.l.)	Age (years)	BA (m ² ·m ⁻¹)	PM	C stocks (Mg·ha ⁻¹)								Source
						Overstory			Roots			Soils		
						Living stems	Needles	Branches	Small	Large	SOL	Mineral	Depth (cm)	
Field studies														
Mountain pine	6	2010	156	25	alkaline	54	2	6	2	9	23	91	0–20	This study, Switzerland
Mixed conifers	5	1790	187	42	alkaline	116	4	8	3	34	16	54	0–20	This study, Switzerland
Stone pine – larch	3	2040	223	44	alkaline	131	3	11	3	36	19	54	0–20	This study, Switzerland
Stone pine – larch	4	1980	223	50	acidic	131	3	11	3	45	20	29	0–20	This study, Switzerland
Norway spruce	6	1700–1750	–212*	—	alkaline	–260	—	—	—	—	–27	–85	0–50	Thuille and Schulze 2006, Italy
Norway spruce	1	1740	—	14	acidic	~ 54 [†]	—	—	—	—	—	115	0–30	Rodeghiero and Cescatti 2005, Italy
Larch – Norway spruce	1	1750	<30	—	acidic	~ 33 [†]	—	—	—	9 [‡]	3	—	—	Gamper et al. 2007, Italy
Stone pine	1	1950	100	47	acidic	—	—	—	—	—	—	—	—	Wieser and Stöhr 2005, [§] Austria
Modeled estimates														
Pine	—	1800–2200	—	—	—	127	—	—	—	—	—	—	—	Erb 2004, [¶] Austria
Conifers**	—	—	—	—	—	36–71	2–4	13–20	~ 1	23–29	12–18	37–58	0–20	Perruchoud et al. 1999, [¶] Switzerland

Note: BA, basal area; PM, parent material; SOL, soil organic layer; Depth, sampling depth of mineral soil.

*The authors studied a chronosequence of naturally established Norway spruce stands with stand ages 14, 37, 54, 78, and 112 years and a 212-year-old control stand.

[†]Total for tree, shrub, and understory.

[‡]Total belowground phytomass.

[§]Only biomass values are given, see text.

^{||}Species not given.

[¶]Modeled based on inventory data, no sampling.

**Coniferous forests of the Pre-Alps, Alps, Southern Alps; elevation range or tree species not given.

ecosystem C stocks between the abandoned pastures and early successional forest ecosystems, which was similar to findings by Thuille and Schulze (2006) and Gamper et al. (2007) for high-elevation sites in Italy. The differences found in our study were, however, only due to differences in aboveground C stocks, as belowground C stocks did not significantly differ between the pastures and the early successional mountain pine forests. Literature reviews by Guo and Gifford (2002) and Paul et al. (2002) showed for low-elevation sites that depending on time since land abandonment, the type of forest established, and climate, increased, unchanged, and decreased mineral soil C stocks can be found after forest establishment on abandoned farmland or pastures. Our results as well as the findings by Thuille and Schulze (2006) suggest that reforestation does not significantly affect belowground C stocks at high elevation.

Our study also showed higher aboveground C stocks in mixed-conifer and stone pine–larch stands compared with the mountain pine forests, but as noted earlier, we found no significant differences in belowground C stocks among the forest types. We are aware of only a few field studies that reported biomass or C stocks of high-elevation forest vegetation in Europe (Table 6), while there are many studies conducted at lower elevations (e.g., Thuille et al. 2000). However, all these studies reported C stocks of single stands or used chronosequences of early successional forests, and we could not find any other study that compared C stocks among different stages of long-term forest succession that includes shifts in tree species composition. Additionally, comparing our forest C stocks with the few results available from these high-elevation single stand or chronosequence studies is somewhat problematic, as various contributions of stand and soil components have been used to calculate C stocks (Table 6). Thuille and Schulze (2006) only reported C stocks in beechwood of their 14- to 212-year-old Norway spruce / silver fir (*Abies alba* Miller) stands in northern Italy, while Rodeghiero and Cescatti (2005) and Gamper et al. (2007) gave one aboveground total C stock value for tree, shrub, and understory combined. Mineral soil depth used in belowground C stock calculations ranged from 20 cm in our study to 30 cm and 50 cm in other studies (Table 6), which has a large impact on belowground and total ecosystem C stock estimates. In addition to field studies, several estimates of high-elevation C stocks have been derived from forest inventory information. Erb (2004) used forest inventory data to simulate aboveground C stocks for mature pine–larch forests of the Austrian inner-alpine climate zone, and Perruchoud et al. (1999) used SNFI data to model forest vegetation and soil C stocks in Switzerland, including the Alps (Table 6).

As discussed above, mineral soil C stocks were higher in mountain pine stands than in mixed-conifer and stone pine–larch stands. The early succession mountain pine forests had the highest cover of ericaceous shrubs, which decreased in later successional stages. Leaves, roots, and mycorrhizae of ericaceous shrubs decompose very slowly, owing to high amounts of phenols, lignin, organic acids, and low nitrogen (N) concentrations (Read 1991; Nilsson and Wardle 2005). Generally, decomposition rates of plant material are closely related to lignin and N concentrations and decomposition stage (e.g., Taylor et al. 1989; Berg and

Meentemeyer 2002). Thuille and Schulze (2006) reported higher mineral soil C stocks in Norway spruce stands in Germany and Italy when ericaceous shrubs were present. It is also possible that different photosynthetic rates among our tree species could affect the proportion of net primary production transferred to the mineral soil through root exudation, fine root turnover, or mycorrhizae (Clark et al. 2001). For example, Tranquillini (1979) showed that stone pine stored more annual net C than larch, and Zarter et al. (2006) found significant differences in the photosynthetic rates of five tree species growing at high elevations in Colorado. Similarly, the turnover rates of coarse roots could differ, as the maximum tree age of the dominant species increases from early to late successional stages. Larch, stone pine, Norway spruce, and Scots pine trees can reach ages of 600–1200 years, while the maximum age of mountain pine is only 300–500 years (e.g., Bernatzky 1978; Mayer 1992). Therefore, longer lifespan of coarse roots and slower turnover times could also be a factor in the lower mineral soil C contents in our mixed-conifer and stone pine–larch stands.

C sequestration

Our study indicates that reforestation of abandoned, high-elevation pastures by mountain pine would lead to a mean increase in total ecosystem C stocks of approximately 120 Mg·ha⁻¹. Using a mean mountain pine stand age of 156 years, these stands would have a mean yearly C sequestration rate of approximately 0.76 Mg C·ha⁻¹ since establishment. This rate is within the range of 0.57–0.8 Mg C·ha⁻¹·year⁻¹ reported from net ecosystem exchange measurements in a high-elevation subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stand in Colorado during a dry and a “normal” year between 1998 and 2000 (Monson et al. 2002). We are aware that our rates are long-term averages, but we could not find information on differences in biomass or C stocks in different aged mountain pine stands in the literature.

Information from both the first and second SNFI shows that approximately ~0.4%–0.7% of Switzerland's 570 000 ha agricultural land and nonforest vegetation (wetlands, riparian areas, shrublands) located above 1650 m a.s.l. are reforested each year (Brassel and Brändli 1999; Swiss Federal Statistical Office 2004). Using our mean yearly values of 0.76 Mg C·ha⁻¹ increases in ecosystem C stocks, 1733–3032 Mg C·year⁻¹ would be added to the total Swiss forest C sequestration due to high-elevation land abandonment each year. Given that Swiss forests sequester approximately 1 600 000 Mg C·year⁻¹ based on calculations by Perruchoud et al. (1999), who used forest inventory data, C sequestration as a result of natural reforestation of high-elevation land can likely be considered as negligible at a national level when discussing potential strategies for increasing the amount of C stored in soils and vegetation of different ecosystems. Also, based on our results, establishing forest reserves in high-elevation forests of diminishing economical interest as a means of increasing C stocks under Article 3.3 of the Kyoto protocol (United Nations Framework Convention on Climate Change) would not lead to increased ecosystem C storage.

The results of our study are likely applicable to other aban-

doned pastures within the Central European Alps and may apply to other high-elevation forests. While climate, parent material, and management practices would be different in other ecosystems, our protocols, experimental design, and results gained from the forest ecosystems under study may also be useful in designing ecosystem studies on C accumulation and cycling in forests with similar ecological characteristics, such as the successional transition from lodgepole pine to whitebark pine (*Pinus albicaulis* Engelm.) in North America, or from Scots pine to Siberian pine (*Pinus sibirica* Du Tour) in Russia.

Conclusions

Our study is the first investigation based on field data that assessed changes in C stocks during long-term ecosystem development after land-use change in high-elevation ecosystems. When abandoned pastures in the SNP are reforested, C accumulated during early forest succession, but no significant amounts of ecosystem C were added during long-term secondary forest succession. Previous studies on changes in OM and C stocks were conducted in early successional forest stands, but did not address the changes taking place during later successional stages. While C sequestration in these high-elevation Swiss ecosystems was appreciable, it would likely have a negligible impact on C sequestration at the national scale, since the naturally reforested areas are small. However, our results likely are applicable in other areas of the Central European Alps and may apply to other high-elevation forests where tree species with similar ecological characteristics grow. Additional studies on long-term C changes during secondary succession are needed to determine whether our results are representative of successional pathways after land abandonment in other regions and elevations.

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Appendix A Regression parameters for bio-mass calculation

The regression parameters and basic density (dry mass per fresh volume) values for the five tree species for eqs. 1, 3, and 4 used to calculate biomass of large trees (diameter at breast height >7.5 cm; Bio_{large}), branches and twigs ($Bio_{branches}$), and foliage ($Bio_{foliage}$) are listed in Table A1. Table A1 appears on the following page.

Table A1. Regression parameters for eqs. 1 (A), 3 (B), and 4 (C) from Kaufmann (2001, 2002) and basic density (sg_i) values from Trendlenburg and Mayer-Wegelin (1955), Guggenbühl (1962), and Stiftung Arbeitskreis Schreinermeister (1991).

(A) Regression parameters for eq. 1.							
Species i	$a_{0,i}$	$a_{1,i}$	$a_{2,i}$	sg_i	a_i	b_i	c_i
Mountain pine	0.00978	0.37868	-0.09278	0.80	1.13880	0.00791	8.8691E-9
Scots pine	0.00978	0.37868	-0.09278	0.49	1.13880	0.00791	8.8691E-9
Larch	0.02362	0.37185	-0.10275	0.55	1.13880	0.00791	8.8691E-9
Stone pine	0.01850	0.40625	-0.12512	0.44	1.13880	0.00791	8.8691E-9
Norway spruce	0.00926	0.42407	-0.17402	0.43	1.41370	0.02418	-1.0670E-6
(B) Regression parameters for eq. 3.							
Species i	$b_{0,i}^*$	$b_{1,i}^*$	$b_{2,i}^*$	$b_{3,i}^*$	$h_{1,i}^*$	$h_{2,i}^*$	
Mountain pine	-7.71477	0.07229	0	0	0	1	
Scots pine	-7.71477	0.07229	0	0	0	1	
Larch	-5.88712	0.01082	0	0	0	1	
Stone pine	-7.71477	0.07229	0	0	0	1	
Norway spruce	—	—	—	—	—	—	
(C) Regression parameters for eq. 4.							
Species i	$b_{0,i}^\dagger$	$b_{1,i}^\dagger$	$b_{2,i}^\dagger$	$b_{3,i}^\dagger$	$h_{1,i}^\dagger$	$h_{2,i}^\dagger$	
Mountain pine	-1.71524	-0.01391	0	0	0	1	
Scots pine	-1.71524	-0.01391	0	0	0	1	
Larch	-2.27729	-0.00672	0	0	0	1	
Stone pine	-1.71524	-0.01391	0	0	0	1	
Norway spruce	-1.20641	-0.01918	0	0.44296	0	1	

*Branches (no merchantable branches for Norway spruce).

†Twigs.

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Appendix B Carbon (C) concentrations

C concentrations of stem wood and foliage of each species as well as solid and rotten woody residue are presented in Table B1. Surface organic layer (SOL) concentrations, fine roots, and understory vegetation for each ecosystem type are presented in Table B2. Mean C contents for branches and coarse roots were assumed to be 50%. Tables B1 and B2 appear on the following page.

Table B1. Carbon (C) concentrations for tree species specific stem wood, foliage, and woody residue.

	C concentration (%)	
	Stemwood	Foliage
<i>Pinus montana</i>	50.5 (0.8)	51.5 (0.3)
<i>Pinus cembra</i>	52.7 (1.5)	50.3 (0.2)
<i>Larix decidua</i>	48.7 (0.2)	50.3 (0.4)
<i>Picea abies</i>	48.7 (0.1)	50.5(0.2)
<i>Pinus sylvestris</i>	50.6 (0.9)	51.4 0.2)
Woody residue		
Solid	50.9 (0.4)	
Rotten	56.0 (1.3)	

Note: Values are means of all samples. Values in parentheses are SEs.

Table B2. Mean C concentration in understory vegetation, surface organic layer (SOL), and fine roots per ecosystem type.

Ecosystem type	C concentration (%)		
	Understory vegetation	SOL	Fine roots
Short-grass pasture	44.2 (—)	28.4 (1.1)	37.5 (1.3)
Tall-grass pasture	45.0 (—)	27.0 (1.7)	37.2 (0.5)
Mountain pine	49.9 (0.9)	40.0 (1.4)	45.6 (0.5)
Mixed-conifer	49.6 (1.2)	36.2 (3.2)	39.5 (1.8)
Stone pine–larch (alkaline)	48.0 (0.4)	36.4 (1.5)	40.8 (1.4)
Stone pine–larch (acidic)	49.2 (1.0)	36.2 (3.9)	44.9 (1.7)

Note: Values in parentheses are SEs.